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Structure of the Columella auris in the Polycosauva

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In a specimen of the Permian reptile *Clepsydrops leptocephalus* Cope,* the columella auris was found nearly in its normal position. It was found lying on the internal side of the normally joined squamosal and quadrate bones, the greater part of it within the former, but the distal extremity overlapping the superior part of the latter. These elements have lost their attachment to the cranium proper, so that the connection of the columella with the latter is not visible.

The columella is of unusual size as compared with other bones of the skull. Thus while the vertical length of the premaxillary bone is M. .060, and its width at the third tooth is .022, and while the vertical length of the quadrate bone is .085, the dimensions of the columella auris are as follows:

Length on inside of curve		.072
Greatest diameter just below stapes		.021
Distal diameters	long	.014
	short	.011
Diameters of head of epicolumella	long	.017
	short	.0095
Diameters of disk of stapes	long	.029
	short	.021

The shaft is slightly curved. The proximal extremity is divided by a fissure which is at right angles to the long transverse diameter. The smaller of these divisions is the more prominent, and its free extremital angle is formed by the continuous concave edge of the shaft. It bears the same relation to the shaft as the head of a rib does to its shaft (Fig. 1). The other proximal division occupies the position with reference to the shaft that the tubercle does to the rib. It is much larger than the inner head of the columella, and its face looks away from that of the head at an angle of 120°. Its long diameter diverges from that of the head by an angle of about 145°. Its free surface is a wide oval, and is concave, forming a basin-shaped lid to the foramen ovale of the internal ear. It thus represents the expanded proximal extremity of the stapes of other vertebrates. The base of this stapedial portion is perforated in the direction of its long diameter by a canal. One foramen of this canal is situated on the external edge below the external extremity of the oval basin. The other foramen issues in a groove, which continues for a short distance on the inner side of the bone from the fissure which separates the epicolumella from the stapes. This canal is, no doubt, that for the mandibular artery, and represents the foramen of the stapes, which is present in many Mammalia (Fig. 1 e e).

The distal extremity of the shaft is concave, and shows an articular surface of ridges and pits (Fig. 1 c). The coarseness of the latter indicates that the distal element attached at this point was cartilaginous, at least at the point of attachment. It will then resemble the corresponding part in the Crocodilia and Lacertilia, which connects the columella with the membranum tympani.

The points above determined as to the structure of this element permit of a number of interesting deductions.

First. This columella possesses what has not been previously observed in reptiles and higher

* Proceedings American Philosophical Society, 1884, p. 30.

vertebrates, an osseous connection, distinct from that formed by the stapes with the foramen ovale of the os petrosum. From this it follows that the stapes cannot be regarded as the proximal extremity of the visceral arch of which the columella forms a part, as its appearance in other reptiles would lead us to infer. It also lends support to the view of Salensky, which is accepted by Fraser, that the stapes is not an ossification of the cartilage of the visceral arch, but is an ossification of the tissue surrounding the mandibular artery.

Second. That the stapes resembles that of the Mammalia, and differs from that of other reptiles in the perforation below its head.

Third. That it is succeeded distally by a cartilaginous element, as in many other reptiles, which is the triangular ligament of Cuvier, and is functionally the analogue, and probably the homologue of the malleus of the Mammalia.

The homology of the proximal extremity of this columella may now be considered. It cannot be the suprastapedial cartilage of Huxley, since that is a superior process of the distal cartilaginous element or malleus. It appears to be unrepresented in the reptilian columella, and I have therefore called it the *epicolumella** (Figs. 1, Ecol).

In order to obtain some light on the homologies of the parts of this element, I have compared it with the corresponding parts in various species of reptiles and batrachians, several of which have been figured by Messrs. Huxley, Peters, and Parker. I have examined the ear bones and cartilages of the *Heloderma suspectum*, and append herewith the result of my observations:

The columella has the length usual in the Lacertilia, ceasing a short distance proximad to the eustachian foramen. The cartilage, which continues in the same straight line, is divided at the eustachian foramen, one process passing downwards on its anterior border, the other forming its superior border. The posterior branch continues downwards for a short distance and terminates in a point, which is connected by a short ligament with the extremity of the pterygoid bone (Fig. 2 hl). Immediately exterior to it, a slender, rod-like ligament descends in close contact with it. It extends farther, however, reaching the articular bone of the lower jaw immediately posterior to the cotylus for the quadrate (Fig. 2 el). Its subsequent course will be mentioned below. It appears to be the ligament which Peters has represented as continuous with the descending process of the stapedial cartilage, and on which he based his belief in the continuity of the latter with the cartilage of Meckel. Its superior connection is, however, not with any part of the ossicula auditus, but it can be traced to a point above the external extremity of the exoccipital bone.

The stapedial cartilage extends beyond the superior edge of the large eustachian foramen to the membranum tympani, and is there decurved, extending in contact with it for 2–3 mm. and terminating in an acute apex. Near the point where it reaches the membrane it sends a branch upwards and backwards (Fig. 2 sst,) the suprastapedial cartilage, which forms a slender rod. The suprastapedial reaches inwards, and terminates at a point on the inferior side of the exoccipital bone at a point a little within opposite the origin of the inferior branch. It is only connected with the horizontal cartilage below it by membrane, and it does not form a fan-shaped plate as represented by Peters in Stellio and Huxley in Hatteria.

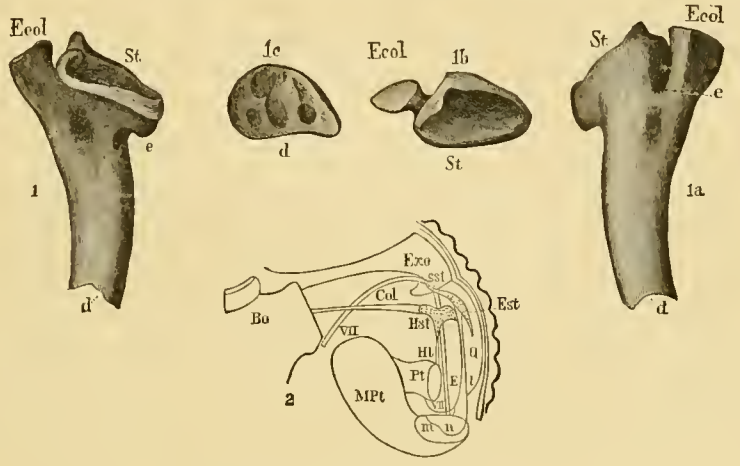
The following are the connections of the cartilages with adjacent elements: The distal extremity is acuminate and lies for a short distance on the membranum tympani, where it terminates without continuation. From the convexity of the curve formed by the inferior edge of the cartilage where it turns upwards, backwards, and inwards to form the suprastapedial, a narrow and weak band descends. It passes along the posterior border of the eustachian foramen, and terminates on the superior edge of the mandible. As it descends it thins out and becomes undistinguishable as a distinct rod or band. The slender rod already described as descending to the mandible from the descending process of the cartilage along the inner border of the eustachian foramen is figured by Peters in *Uromastix spinipes*.† He describes "it as a fibrous thread, which was formerly cartilaginous and connected the malleus with Meckel's cartilage." According to the figure it is not continuous with the inferior process of the cartilage ("malleus"). In *Heloderma suspectum* it passes anterior to the cartilage, in close contact with it, to a point superior to the suprastapedial process,

*American Naturalist, 1884, p. 1254.

†Monatsberichte Akademie Berlin, 1874, 44 f. B.

and then turns towards the base of the skull. I trace it directly to a foramen on the superior edge of the sphenoid. It is clearly the facial portion of the seventh nerve (tensor tympani), as described by Fischer and Stannius,* and has nothing to do with the auricular bones and cartilages. The only connection, then, with inferior arches which I can detect in this species is the fibrous one with the mandible, and I am doubtful of the significance of this.

It does not seem practicable to recognize the suprastapedial in the epicolumella of *Clepsydrops leptocephalus*.† It would require an excessive shortening of the columella, which might readily be the condition of things in Clepsydrops. But it would require that the suprastapedial should be ossified, and separated by suture from the remainder of the cartilage. Until some form is found in which this cartilage is segmented such a hypothesis has no foundation. The homology of the epicolumella with the incus is, on the other hand, almost certain; *first*, by the evident propriety of the exclusion of the stapes from the question, on account of its position, and by the history of its origin as shown by Salensky; *second*, on account of its position relative to both the stapes and the malleus. This being the case, the result follows that the doctrine of Peters that the quadrate bone is not the incus, as was maintained by Reichert, is the true one.‡



EXPLANATION OF PLATE.

FIG. 1. Columella auris of *Clepsydrops leptocephalus;* internal side. Fig. 1*a*, external side; 1*b*, proximal extremity; 1*c*, distal extremity; st., head of stapes; *Ecol.*, epicolumella; *d*, distal articular surface, especially represented in Fig. 1*c*; *c e*, foramina of stapedial canal. All figures are half natural size, excepting 1*c*, which is natural size.—From the proceedings of the American Philosophical Society, 1884, p. 46.

FIG. 2. Auricular bones and cartilages and adjacent parts of *Heloderma suspectum* Cope,§ twice natural size. *Bo.*, basioccipital bone; *Exo.*, exoccipital; *Q.*, quadrate; *Mn.*, mandible; *Pt.*, pterygoid; *M. Pt.*, internal pterygoid muscle; VII, seventh nerve; *Col.*, columella auris; *Hst.*, hypostapedial process of auricular cartilage; *Sst.*, suprastapedial process; *Est.*, epistapedial process; *Hl.*, hypostapedial ligament; *El.*, epistapedial ligament.

* Zoötomie der Fische, p. 154.

† Such a hypothesis is suggested after inspection of Huxley's figure of these parts in Hatteria, in Anatomy of Vertebrated Animals, p. 77, Fig. A. See also American Naturalist, 1884, p. 1253; Proceeds. Amer. Philosoph. Soc., 1884, p. 41.

‡ See Proceedings Amer. Philosoph. Society, 1884, p. 41, where Peter's view is maintained.

§ I owe the specimen dissected to my friend Horatio N. Rust, who obtained it on the Gila River, Arizona.